Table 1. Results of three experiments on microsomes and the supernatant from the centrifugation at 105,000g. Valine-2,3-H3 with an activity of 400 mc/mmole was used as the tracer. Activity measurements were converted to decompositions per minute (dpm) per milligram of protein per milligram of protein in the ribosomal suspension by addition of an internal standard.

Source		10-4	
Microsomes	105,000g Supernatant	dpm	
Control	Control	$1.63 \pm 0.10$	
Control	Treated	$1.75 \pm 0.21$	
Treated	Control	$0.35 \pm 0.17$	
Treated	Treated	$0.35 \pm 0.17$	

incubated with the liver supernatant fraction from control or experimental animals, and microsomes from experimental animals were incubated with supernatant from control or experimental animals. The results of this series of experiments (Table 1) are expressed as decompositions per minute per milligram of protein per milligram of protein in the microsomal suspension. This was done in order to account for variations in concentrations of microsomal suspensions from experiment to experiment. The data show that the depressed rate of incorporation of amino acids into microsomal material is a property of the microsomes of the CCl<sub>4</sub>treated animals regardless of the source of the supernatant material containing the activating enzyme, the transfer enzyme, and the sRNA. Furthermore, it is apparent that the supernatant material isolated from CCl<sub>4</sub>-treated animals does not inhibit the capacity of the microsomes of control animals to incorporate amino acid.

The previous data, designating the ribosomes as the site of a change induced by CCl<sub>4</sub>-intoxication, suggested examination of the physical properties of the ribosome. After intoxication of the animals, there is in the liver extracts a marked decrease in the relative concentration of material in the 79S peak and an increase in the slower 54S fraction (Fig. 1). In repeated analyses the decrease in the 79S peak appears equal to the increase in the 54S peak without significant changes in either the faster or slower sedimenting components.

The evidence now seems secure that ribosomes are the structures common to all cells where the ultimate assembly of amino acids into protein takes place. Moreover, ribosomes from organisms as varied as Escherichia coli, pea seedling, rat liver, and rabbit reticulocytes all seem to be composed of a series of particles, and the sizes of particles from each of these sources are similar. The larger particles appear to be formed of aggregates of the small particles and the distribution of particle populations can be reversibly altered (15). Finally, it has been found that the capacity of a ribosomal preparation to incorporate amino acids is dependent upon the state of aggregation of the particles. In particular, active incorporation of amino acids appears to be associated with the presence of the larger aggregates, 79S or greater. The effects of CCl4, administered in vivo, on rat-liver ribosomes provides new evidence to substantiate these views.

The apparent dissociation of 79S particles into 54S particles, indicated by the reciprocal increase in the latter in the CCl<sub>4</sub>-treated animals, seems to indicate that some special part of the cellorganelle structure is affected by the CCl<sub>4</sub>. Experiments in which CCl<sub>4</sub> was applied to the homogenate in vitro did not produce a similar alteration in the sedimentation pattern. Hence the chemical defect does not appear to be a simple physical solvation of the ribosome. The ultimate chemical nature of the change produced in the ribosomes by  $CCl_4$  remains to be discovered (16).

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## All-or-None Learning and the Role of Repetition in **Paired-Associate Learning**

Abstract. The learning of a list of stimulus-response items is a two-stage process involving response learning and association. It is assumed that both stages are learned in an all-or-none fashion. Subjects were trained to learn a list of pairedassociate items with Rock's substitution procedure. Their performance could be predicted from the all-or-none theory with parameter estimates based upon the performance of a different group of subjects who learned the same items under normal conditions.

In paired-associate learning the learning material is arranged in pairs consisting of a stimulus item and a response item. The stimulus-response pairs are first presented together and then the stimulus item is shown alone and the subject is asked to give the response item. Normally item pairs are repeated until the subject always gives the correct response. With the substitution procedure, however, an item pair is replaced with a new one whenever the subject fails to give the correct response.

Rock (1) found that this procedure did not retard learning when compared to the usual procedure of repeated presentation of all items. From this finding he concluded that learning was not gradual but an all-ornone phenomenon, since replacing "wrong" items should lead to slower learning if learning were incremental. The idea of all-or-none learning has achieved a certain popularity in the meantime, but Rock's initial evidence has been questioned by recent investigators. A process of item selection confounded the results obtained with the substitution procedure. Difficult items were not learned and were therefore replaced by new items in the substitution condition, but in the control group subjects had to master all associations. Thus the subjects in the substitution group learned, in effect, an easier list than subjects in the control group.

It now appears that the substitution procedure retards learning whenever proper control groups are used to account for the effects of item selection (2) or when these effects are minimized by the use of items which are very homogeneous in difficulty (3). The present report attempts to show that this result not only does not contradict an all-or-none theory of learning, but can be quantitatively predicted from such a theory. The model proposed here uses the finding that the learning of a stimulus-response pair is a two-stage task (see, for example, 4). First, the response must be learned and then it can be associated with the proper stimulus. It is assumed here that both of these processes occur in an all-or-none fashion. Such a model will, of course, predict impairment of learning under the substitution procedure because items will sometimes be discarded after the response has already been acquired though not yet hooked up to the correct stimulus.

Consider a three-state Markov process. The two stages, response learning and association, correspond to two transitions, first from a state Co of no learning to a state C1 where the response is learned but not yet connected to the right stimulus, and then from state C1 to state C2 when the association occurs. Let p represent the probability of a correct response to an item for which only response learning has occurred. Then the probability that the correct response will be given to a stimulus will be 0, p, or 1 in states  $C_0$ ,  $C_1$ , and  $C_2$ , respectively. These assumptions are expressed in transition matrix Q, where for reasons of mathematical convenience the state C1 has been subdivided, depending upon whether the subject makes an error (with probability 1 - p = q) or a success (with probability p).

$$Q = \begin{array}{c} C_0 & C_{1e} & C_{1s} & C_2 \\ C_1e & C_{1s} & C_2 \\ C_{1s} & C_2 \end{array} \begin{bmatrix} C_0 & C_{1e} & C_1s & C_2 \\ 0 & (1-e)q & (e-e)p & e \\ 0 & (1-e)q & (1-e)p & e \\ 0 & (1-s)q & (1-s)p & s \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

The four parameters of the model are c, the probability of response learning, e, the probability of association after the subject has made an error in state C<sub>1</sub>, s, the same probability after a success, and p, as defined above (5). This 19 APRIL 1963

Item	Predicted	Observed
Mean number of errors per item	3.79*	3.79
Standard deviation	2.45	2.15
Mean number of trials before the first success Standard deviation	3.40* 2.42	3.40 2.01
Mean trial of last error	4.15	4.29
Standard deviation	2.92	2.76
Mean number of error runs per item	1.26	1.27
Number of error runs of length 1	.40	.32
Number of error runs of length 2	.27	.30
Number of error runs of length 3	.20	.26
Number of error runs of length 4	.13	.16
Number of error runs of length 5	.09	.07
Number of error runs of length 6	.06	.07
Number of error runs of length 7	.04	.05

\* Used for estimation.

model is based upon Estes' "two element pattern model" and was first employed and described in detail by Bower and Theios (6). The model implies that as long as a subject is in state C<sub>1</sub> successes will occur with probability p, independent of what happened on the previous trial. A great number of predictions concerning various statistics of the data are also implied. For instance, the first row of the matrix  $Q^n$  contains the probabilities of being in each one of the states Co, C1s, C1s, and C2 on trial n, since the process always begins in C<sub>0</sub>. The predicted proportion of errors on that trial will then be the sum of the first two of these terms, since errors can only be made in C<sub>0</sub> and C<sub>1e</sub>.

All predictions will be expressions involving some or all of the parameters of the model. By setting three of these theoretical expressions equal to their observed values and solving the resulting equations simultaneously for c, e, and s, estimates for these parameters can be obtained (7). Since p is the probability of success after the response has been learned but not yet connected to the right stimulus, the observed proportion of successes on the trials between the first success and the last failure serves as an estimate for it. No desirable statistical properties of these estimates are known, but they are acceptable in the sense that a fairly good fit of the model is achieved with them.

When the substitution procedure described above is used, Q will no longer be a correct representation because with probability 1 the subject returns from state  $C_{1\sigma}$  to  $C_0$ . These two states therefore become indistinguishable and the transition matrix characterizing the substitution condition can be written as

$$Q^* = C_0, C_{1e} \begin{bmatrix} C_0, C_{1e} & C_{1s} & C_2 \\ (1-c)+cq & cp & 0 \\ C_{1e} & (1-s)q & (1-s)p & s \\ 0 & 0 & 1 \end{bmatrix}$$

Several predictions about subjects' behavior under the substitution procedure can be derived from  $Q^*$ . For example the mean proportion of errors on trial n will be given by the upper left-hand entry in the matrix  $Q^{*n}$ . These predictions are made without using any of the data for parameter estimation. Instead, estimates for c, s, and p were obtained from matrix Q, that is, from the behavior of a separate control group which learned the same material under normal conditions. These estimates should predict the behavior of the experimental group when inserted into  $Q^*$  if the two transition matrices given above correctly represent the situation.

In order to test these predictions two groups of 23 subjects each were given a list of paired-associate items to learn. The items were two-place numbers paired with nonsense syllables. The syllables were of about 55-percent association value and pairs were selected for homogeneity on the basis of a rating procedure (8). Each subject learned a list of eight randomly selected pairs. A trial consisted of a presentation of the eight pairs, each for 4 seconds, during which the subject read the number-nonsense syllable pair aloud. Immediately afterwards each stimulus number was presented alone for 4 seconds and the subject was asked to give the proper response. The order of items was randomized for each presentation. Learning in the control group was continued to a criterion of three successive correct trials. For the experimental group the substitution procedure was used, that is, whenever a subject did not give the correct response on a test trial the item was replaced by a randomly selected new number-syllable pair. Ten trials were given. In order to acquaint the subjects in both groups with the experimental procedure they were given

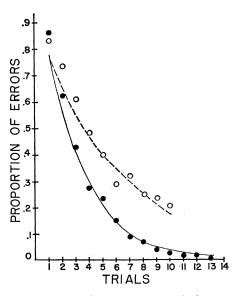


Fig. 1. Proportion of errors made by experimental subjects (open circles) and controls (solid circles). The smooth curves are the predictions derived from the two-stage model.

practice trials with a six-syllable list until they reached a criterion of one errorless trial.

The most important results of this experiment are presented in Fig. 1. The substitution procedure retarded learning in the amount predicted by the two-stage model. The theoretical curves in Fig. 1 were obtained by estimating the parameters of the model from the data of the control group (c = .35, s =.55, e = .17, p = .61). The predicted mean learning curve for the experimental group was then computed by inserting these values into  $Q^{*n}$ . Considering that no data from the experimental group were used for this prediction, the fit is quite good. The occurrence of more errors than predicted during the first few trials in both the control and experimental groups might possibly be due to a warm-up effect in the experiment because of insufficient pretraining.

The probability of an item being replaced after one or more correct responses was .29; predicted was .24. Apart from predictions concerning the experimental group, the model can also be used to describe the behavior of the control group. The crucial point here is the prediction that successes in state  $C_1$  will be independent events, emitted with a stationary probability *p*. On trials between the first success and the last error subjects must be in state  $C_1$ . A Vincentized learning curve based upon responses on these trials reveals that the proportion of errors decreases from .39 in the first half of the trials to .36 in the second, which is far from being statistically significant ( $\chi^2 = .12$ ). A test for independence also led to a nonsignificant  $\chi^2$  value ( $\chi^2 = 1.47$ , one degree of freedom). These results are in good agreement with the model but they are based upon too small a portion of the data, since, owing to the generally fast learning, many items did not have any responses between the first success and last error. Statistics which are based upon all items with their predictions derived from the twostage model are given in Table 1.

The results of the present experiment were completely confirmed in a second experiment. The two-stage model predicted 5.09 errors per item during the first 10 trials in the substitution condition; 5.16 were observed. Again, this is a true prediction, since no data of the experimental group were used for parameter estimation. The only difference between the two experiments was that in the second experiment subjects were not required to read all items aloud. This experiment was therefore more open to the criticism that any observed all-or-none behavior simply reflected the fact that subjects could concentrate upon a few items at a time.

In spite of the successful predictions derived from the present model, a major problem remains. What has proved its usefulness here is a two-stage Markov model. The interpretation given to the two stages in terms of response learning and associative stages has not been tested directly. In order to do this, it would be necessary to show that the parameters of the model are differentially affected by experimental manipulations of the amount of response learning required and the difficulty of association (9).

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- 7. The expressions used are the mean number of errors, the mean trials before the first success, and the mean number of times a success is followed by an error. For details of the estimation procedure as well as for the derivation of other predictions see Bower and Theios (6).
- This procedure resulted in quite a homogeneous item pool. Only very little evidence of item selection due to differential difficulty was found in the present experiment.
   The assistance of Jacqueline Bragg and Don
- 9. The assistance of Jacqueline Bragg and Don McCoy in collecting part of the data is acknowledged. This research was supported by NSF grant GB-195.
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**Evaporation Enhancement by Protein Films** 

Abstract. Evaporation of water takes place more rapidly from buffered solutions of ovalbumin or hemoglobin than from solutions of certain surface-active agents or from buffer alone. The effect appears to be connected with adsorption of protein.

It is well known that films of surfaceactive substances can reduce the evaporation of water. Practical use is made of such films in large-scale projects for slowing water loss from reservoirs by application of monolayers of hexadecanol or similar substances (1). In addition, Deryagin et al. have shown mathematically and experimentally that surface films can actually increase the evaporation rate of water under certain special conditions (2). Furthermore, Bull found that constantly renewed adsorbed films of ovalbumin appeared to increase greatly the evaporation of water (3). He found no significant effects when the surfaces were motionless, however. The latter experiment was

carried out by placing dishes of water and protein solutions overnight in a desiccator, with evaporation rates being determined from the loss in weight of the dishes and their contents (4).

Langmuir and Schaefer have discussed evaporation as a kinetic process involving successive steps (5). These are transport of water molecules to the surface, passage across the surface region, and diffusion through a quiescent layer of air overlying the liquid surface. Archer and LaMer have considered the energy barriers to each of these processes in terms of a number of resistances (6). One result of this analysis is that if a single resistance is much greater than the others, it com-

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